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ADAPTIVE RESPONSES OF THE WILLOW GROUSE (Lagopus lagopus) TO PREDICTABLE SUBARCTIC CONDITIONS

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SUMMARY

Morphological and anatomical adaptive features of 205 willow grouse (Lagopus lagopus) killed in Finnish Forest Lapland were studied in the course of one year. Seasonal changes were found in net body weight, weight of plumage, liver and kidneys, and in the lengths of small intestines and caeca. Variations also occur in other characteristics of the plumage. Willow grouse appear to be well adapted to predictable seasonality in the environment. Rapid changes do not take place other than in glycogen storage in the liver. No unnecessary adaptation measures are maintained. The field observations emphasize the importance of unpredictable factors in the northern environment with respect to fluctuations in the population of the willow grouse. Weather conditions appeared to play a decisive role among these factors.

INTRODUCTION

The willow grouse (Lagopus lagopus) is the most abundant tetraonid in the subarctic and north-boreal zone

of northern Europe. Its populations are known to fluctuate widely from year to year (e.g. Siivonen, 1957) which is reflected in the trapping success of the local people. The prevailing weather conditions have been regarded as "unpredictable", but there are also "predictable" characteristics, such as seasonality. In winter the substantial snow cover restricts the diet of willow grouse to fibrous food, whilst in summer, with almost snowless conditions more digestible food matter is available (berries, flowers, etc.). The purpose of the present paper is to describe the adaptive responses which the willow grouse has developed to these predictable characteristics of its environment. It is hoped that such an approach may reveal some aspects of the role of unpredictable factors in the population fluctuations seen in this species.

MATERIAL AND METHODS

The study was carried out in Finnish Forest Lapland, on the border of the boreal coniferous forests and subarctic mountain birch forests. Records of the weight of the body (without crop contents), the liver, kidneys and plumage along with lengths of the small intestines and caeca were taken from 205 willow grouse killed during one year. Other observations were also made on their morphology and anatomy.

RESULTS

The main findings were:

1. Since earlier work had shown that there are differences in weights between willow grouse from different areas (Pulliainen, 1968),

relative figures are used here to represent seasonal changes in weight. The mean weights for each period are compared with the yearly mean for each sex and age group (Fig. 1). Overall, birds lost weight during the course of the winter (Fig. 1), but gained weight again in the late winter, before the sexual organs developed in mid-April. This increase was followed by a decrease in relative weight until the summer. This pattern could be expected, since the weight increase takes place prior to the mating season, a period characterized by energy consuming activities.

2. The weight of the plumage (without primaries, secondaries and tail feathers) as a percentage of the total net weight of the body is lowest in summer and autumn, and greatest in winter (Fig. 2E). Presumably its insulation properties are also better in winter than in summer, since the lower critical temperature is -6.3°C during winter and +7.7°C during the summer (West, 1972). The willow grouse appeared to have an almost featherless patch on its flanks under the wings in summer, which probably facilitates heat loss, since a "panting" willow grouse will sit with its wings raised. The bird has many more feathers on its toes and tarsus in winter than in summer.

3. The weight of the liver as a percentage of the total net weight of the body is greatest in late summer, when glycogen is being stored in the liver (Pulliainen & Tunkkari, 1984).

There is no difference in the water content of the liver between summer and winter. Great individual differences exist in the relative weight of the kidneys. A significant minimum in the mean weight was recorded in spring (Fig. 2D), but the reason for this is still unknown.

4. The small intestine decreased in length from late summer to winter and then increased (Fig. 2A). Thus, it is increasing in length when easily digestible carbohydrates (like sugars) are absorbed from the flesh of berries and other corresponding food items. It is longest (Fig. 2A) when large amounts of fibrous food matter are being consumed in winter time (see also Pulliainen & Tunkkari, 1983).

DISCUSSION

The willow grouse appears to be well adapted to a predictable seasonality in its environment. In the extreme north of Europe the snow cover is an inevitable characteristic of the winter period. In this white environment, the willow grouse moults into a white plumage and develops well protected feathered legs and feet. The snow cover restricts the willow grouse to eating fibrous matter, which is difficult to digest, may need detoxification of secondary compounds and must be consumed in great quantities. For this purpose it has developed caeca, whose length can be altered. Smaller individuals have to eat relatively more food than larger ones, and they have relatively longer small intestines and caeca (Pulliainen, 1976). Although the willow grouse spends over four-fifths of a winter's day

in a snow burrow, it is well protected against the cold with a plumage possessing good insulation properties. Since it seeks shelter in snow burrows, it does not require a heart as large as the rock ptarmigan's (Lagopus mutus), which is more exposed to cold winds on the summits of fells and mountains (Pulliainen, 1980).

Since the amplitude of the subarctic winter and summer temperatures may exceed 60°C less insulation is needed in summer than in winter, and an ability to improve heat loss through panting and baring featherless skin is also required. In summer the bird's dark colour and light weight help it to avoid being caught by predators. The species has also developed a system for utilizing berry yields effectively when available by increasing the length of the small intestine, and so increasing the absorbtion surface. Berries may constitute about 60% of the diet in late summer. Glycogen is stored in the liver in summer, but there is no daily glycogen-storing cycle in winter as has been recorded in the rosy starling (Sturnus roseus) (Pilo & George, 1983). This may be because there is enough food stored in the crop to be consumed during rest periods.

Field studies suggest that the egg-laying and incubation periods of willow grouse are not critical in the bird's life cycle (see Pulliainen, 1978), but is when chicks are younger than three weeks old. This is important even though chicks can eat vegetable matter from their first day of feeding (Pulliainen & Eskonen, 1982). For example, in the cold and rainy summer of 1982, practically no willow grouse chicks were found to survive in the southern half of northern Finland despite an intensive search. However, possession of

better insulation and thermoregulation would require greater energy consumption and reduced mobility for the chicks.

The willow grouse may actively select food items (Pulliainen & Salo, 1973), but great variations may occur in the quality of the foods available. Kyllikki Korhonen (pers. comm.) found at one stage that a thick layer of ice had formed on the potential food of the willow grouse (twigs, buds, catkins, etc.), and observed malnutrition in the birds after feeding on this diet. This has also been recorded in the black grouse (Lyrurus tetrix) feeding on a similar diet (Pulliainen, 1982). It is typical that the quantity and quality of the plants available in the north varies from year to year, and thus the potential food for the willow grouse also varies. This appears very clearly in the availability of birch catkins, which are amongst the favourite food items of this species (Pulliainen & Iivanainen, 1981). Flowering in northern plants seems to represent an interaction of two processes, random variation in climate and the effect of the temperature on the accumulation of reserves (Tast & Kalela, 1971). It is supposed that the quality of food eaten is reflected in the outcome of breeding.

These aspects emphasize the importance of unpredictable factors in this northern environment with respect to fluctuations in the population of the willow grouse. Weather conditions play a decisive role among these factors, and can also directly or indirectly affect the risk of an individual falling victim to a predator (see also Myrberget, 1974).

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REFERENCES

Myrberget, S. (1974) Variations in the production of the Willow Grouse, Lagopus lagopus (L.) in Norway, 1963 - 1972. Ornis Scandinavica, 5, 163 - 172.

Pilo, B. & George, J.C. (1983) Diurnal and seasonal variation in liver glycogen and fat in relation to metabolic status of liver and m. pectoralis in the migratory starling, Sturnus roseus, wintering in India. Comparative Biochemistry and Physiology, 74A, 601 - 604.

Pulliainen, E. (1968) On the sex determination and weight of the willow grouse (Lagopus lagopus) in Finnish Lapland. Suomen Riista, 20, 43 - 49.

Pulliainen, E. (1976) Small intestine and caeca lengths in the willow grouse (Lagopus lagopus) in Finnish Lapland. Annales Zoologici Fennici, 13, 195 - 199.

Pulliainen, E. (1978) Behaviour of a willow grouse, Lagopus l. lagopus, at the nest. Ornis Fennica, 55, 141 - 148.

Pulliainen, E. (1980) Heart/body weight ratio in the willow grouse, Lagopus lagopus, and rock ptarmigan Lagopus mutus, in Finnish Lapland. Ornis Fennica, 57, 88 - 90.

Pulliainen, E. (1982) Breeding, foraging and wintering strategies of the black grouse, Lyrurus tetrix L., in the Finnish taiga - a review. Aquilo Ser. Zoologica, 21, 68 - 75.

Pulliainen, E. & Eskonen, H. (1982) Chemical composition of plant matter eaten by young chicks of the willow grouse Lagopus lagopus, in northern Finland. Ornis Fennica, 59, 146 - 148.

Pulliainen, E. & Iivanainen, J. (1981) Winter nutrition of the willow grouse (Lagopus lagopus L.) in the extreme north of Finland. Annales Zoologici Fennici, 18, 263 - 269.

Pulliainen, E. & Salo, L.J. (1973) Food selection by the willow grouse (Lagopus lagopus) in laboratory conditions. Annales Zoologici Fennici, 10, 445 - 448.

Pulliainen, E. & Tunkkari, P.S. (1983) Seasonal changes in the gut length of the willow grouse (Lagopus lagopus) in Finnish Lapland. Annales Zoologici Fennici, 20, 53 - 56.

Pulliainen, E. & Tunkkari, P.S. (1984) Seasonal changes in the weight and composition of the liver of the willow grouse (Lagopus lagopus) in the far north of Finland. Annales Zoologici Fennici, 21, (in press).

Fig. 1 Seasonal changes in the relative net weights of the willow grouse during the course of one year. The mean weights of each period are compared with the yearly mean for each sex and age group.

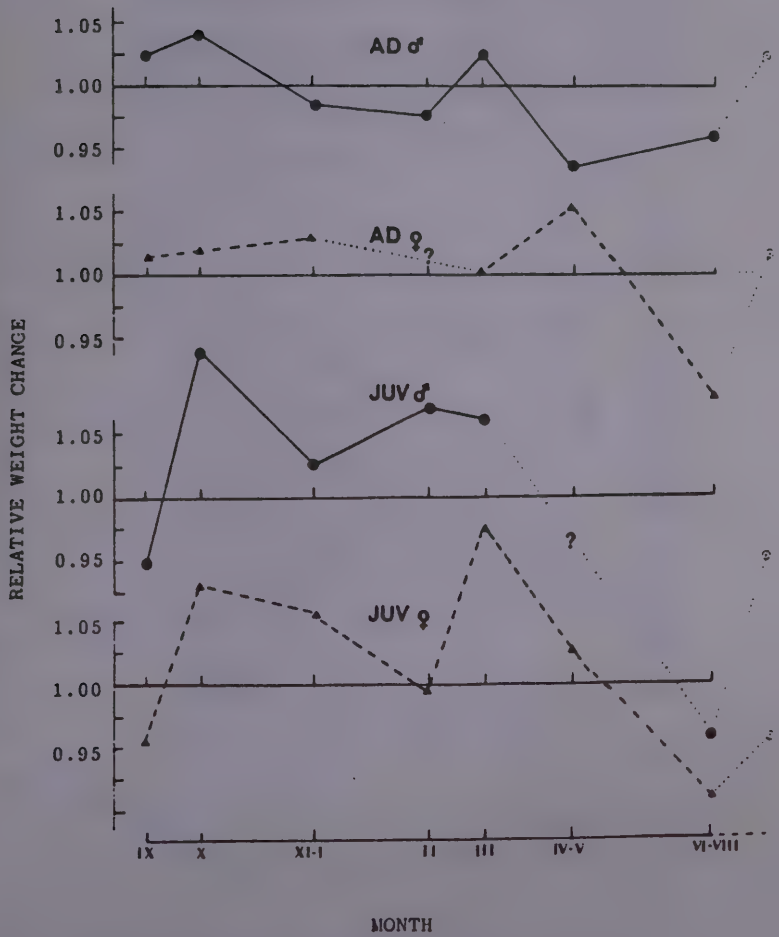
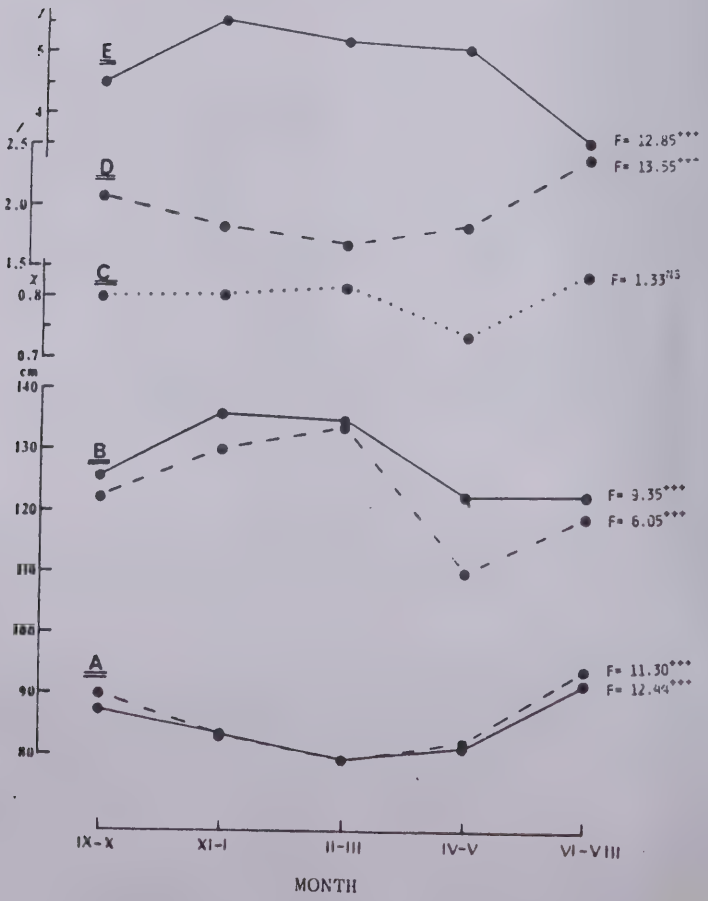


Fig. 2 Seasonal changes in some characteristics of the willow grouse in Finnish Forest Lapland during the course of one year. A = the length of the small intestine, B = the length of combined caeca, C = the fresh weight of the kidneys as a percentage of the total net weight of the body, D = the fresh weight of the liver as a percentage of the total net weight of the body, E = the dry weight of the plumage as a percentage of the total net weight of the body. Solid line indicates adult birds and broken line juvenile birds.



Siivonen, L. (1957) The problem of the short-term fluctuations in numbers of tetraonids in Europe. Papers on Game Research, 19, 1 - 14.

Tast, J. & Kalela, O. (1971) Comparisons between rodent cycles and plant production in Finnish Lapland. Annales Academica Sci. Fennici, A IV 186, 1 - 14.

West, G.C. (1972) Seasonal differences in resting metabolic rate of Alaskan Ptarmigan. Comparative Biochemistry and Physiology, 43A, 293 - 310.

THOMAS I see in your liver data that there is a drop during the time when the females would normally be reproducing. For most breeding species of birds there is a marked increase in the size of the liver at that time. Can you account for this?

PULLIAINEN Can we look at the slide about this?

THOMAS This would be curve D, the curve for the liver? When would breeding be on that graph?

PULLIAINEN The breeding is here and it is lengthening during the breeding season.

THOMAS You are not able to see a marked increase in the liver in that time?

PULLIAINEN No.

THOMAS Why do you think there is a big increase, it's probably about half a percent in the winter?

PULLIAINEN It is decreased during the winter. An increase in the late summer when glycogen is stored.

THOMAS Would that glycogen persist and be used in the winter time?

PULLIAINEN At zero, we have late summer, okay, and it is an increase in size absolutely. We do know because we have recorded deposits in the liver and it is a very clear increase due to storage of

glycoxin in the late summer and then it is decreasing like we see here during the course of the winter and then the increase when soft plant parts are eaten. But I would like to emphasise that there was no day cycle of glycoxin, not at all. Just in mid winter we had permission from the Ministry of Agriculture and Forestry and we used strong lines during the night and killed, shot, the birds throughout the night and recorded glycoxin in the liver and there was no storage at all, but then naturally there was storage of food in the crop.

WEGGE Your graph shows an increase in the weight of the cocks from mid winter to March then a drop. I thought that that was quite interesting, is this when they are eating only birch?

PULLIAINEN Yes, only birch.

WEGGE Have you also noticed a decrease in feeding intensity because of better daylight hours?

PULLIAINEN It must be so; we have recorded the amount of food in the crop when day length is increasing and they are feeding intensively during the daylight period of the day.